Crop Ecosystem Responses to Climatic Change: Rangelands

H. WAYNE POLLEY¹, JACK A. MORGAN²,
BRUCE D. CAMPBELL³ AND MARK STAFFORD SMITH⁴

¹USDA-ARS, Grassland, Soil and Water Research Laboratory, 808 E. Blackland Road, Temple, TX 76502, USA; ²USDA-ARS, Crops Research Laboratory, Fort Collins, CO 80526, USA; ³AgResearch, Grasslands Research Centre, Private Bag 11008, Palmerston North, New Zealand; ⁴CSIRO Division of Wildlife and Ecology, PO Box 2111, Alice Springs, NT 0871, Australia

13.1 Introduction

Rangelands are defined as natural or semi-natural areas that produce plants grazed by wild and domesticated animals (Stoddart et al., 1975). Included in this definition are unimproved grasslands, savannas, shrublands containing both grasses and woody plants, and hot and cold deserts (Fig. 13.1). These ecosystems occur on every continent except Antarctica and cover over 40%

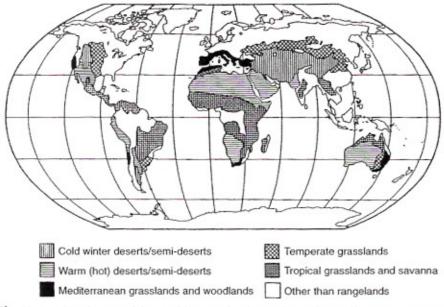


Fig. 13.1. Distribution of the world's rangelands. (Redrawn from Allen-Diaz, 1996.)

of the terrestrial land surface, with the greatest area in Africa and Asia (Allen-Diaz, 1996).

Environmentally determined rangelands are found where climate (chiefly water balance and minimum temperature) and soils interact to prevent occupation by dense stands of trees. Human activities, broadly classified as land use patterns, are another major determinant of the composition and structure of rangelands, and are an example of the alterations to earth considered here as global change. Land use changes include manipulation of fire regimes and other natural disturbances, adjustments in the intensity and duration of grazing, and fragmentation of once continuous rangelands by intensive agriculture and urbanization. Global change also includes changes in atmospheric composition, e.g. carbon dioxide concentration ([CO₂]) and resultant modifications in climate (temperature, precipitation). Some aspects of global change, like atmospheric and land use change, are well underway. Others, including shifts in climate, appear imminent.

Anticipated global changes could dramatically alter the extent and productivity of rangelands, but prediction and risk assessment are complicated by the diverse nature of these ecosystems and varied goals of managers (Campbell et al., 1996; Stafford Smith, 1996).

- Rangelands include a variety of plant species and growth forms (grasses, herbs, trees, shrubs) that respond in different ways and at different rates to the environment and to management inputs.
- Rangelands are spatially and temporally variable. This natural variability increases the difficulty of discerning effects of management from those of the environment and environmental change (Campbell et al., 1996; Stafford Smith, 1996).
- 3. Rangelands traditionally have been used to produce livestock, but these ecosystems provide other 'goods and services', including recreation, water and fuel wood (Fig. 13.2). Atmospheric and climatic change, combined with social, economic and demographic forces, will influence the product or combination of products for which rangelands are managed, and the intensity of future land use.

In this chapter, we review climatic and atmospheric changes expected during the 21st century and suggest some of the consequences of these changes for rangelands that are used primarily for grazing. Non-grazing uses of rangelands are briefly noted to illustrate reciprocal interactions between land use and climatic and atmospheric changes. Finally, we suggest management implications of global change.

13.2 Atmospheric and Climatic Change

The atmospheric $[CO_2]$ has risen during the past 200 years from approximately 280 μ mol mol⁻¹ in pre-industrial times to 360 μ mol mol⁻¹ today, and is projected to double over present-day concentration during the 21st century (Alcamo *et al.*, 1996). Other trace gases (CH₄, N₂O, NO_x, CO) are also

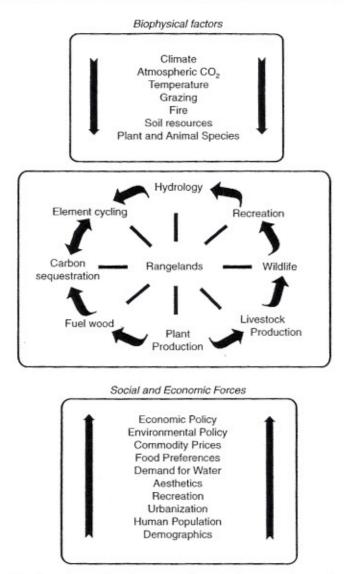


Fig. 13.2. Biophysical, social and economic forces influencing the goods and services for which rangelands are managed.

increasing rapidly, and will contribute to climate change. These increases result from human activities, especially combustion of fossil fuels, land use changes and agriculture. Increases in [CO₂] alone are predicted to warm the earth by 2–4.5°C by the middle of the 21st century, with a resultant increase in precipitation and storm intensity (Giorgi et al., 1998).

Evidence from long-term climatic trends of the last century and modelled effects of [CO₂] (Giorgi et al., 1998; Karl, 1998) suggests that warming will be greatest at high northern latitudes during autumn and winter. Consequently,

temperate grasslands of North America and central Asia may experience relatively more warming than tropical and subtropical grasslands of Africa, Australia, and South and Central America. In high and mid-latitudes, global warming may lead to increased winter precipitation. Predictions are more variable for the tropics, but many models predict more precipitation over India and southeast Asia. Inclusion of aerosols in modelling exercises reduces the change in temperature and precipitation patterns, and sometimes gives regional results that contrast with those obtained by modelling CO₂ responses alone (Giorgi et al., 1998).

13.3 Impacts on Plant Productivity

13.3.1 Atmospheric [CO₂]

Most forage species on rangelands have either the C3 or C4 photosynthetic pathway. Over 95% of the world's plant species, including most woody plants, utilize the C3 pathway. Photosynthesis in C3 plants is not CO2-saturated at the present atmospheric concentration, so increasing [CO2] is predicted to stimulate carbon gain and productivity in these species (Drake et al., 1997). Plants with C4 photosynthetic pathways comprise fewer than 5% of the world's species, but are an important component of tropical and subtropical grasslands (Ehleringer et al., 1997). The final steps of photosynthesis in C4 plants occur in bundle sheath cells, where a highly efficient biochemical pump maintains CO2 at concentrations that nearly saturate photosynthesis when atmospheric [CO₂] is near the current 360 μmol mol⁻¹ (Bowes, 1993). The C₄ metabolism does not, however, preclude photosynthetic and growth responses to CO2 enrichment (Ghannoum et al., 1997; LeCain and Morgan, 1998). Wand and Midgley (1998, unpublished results), for instance, measured a growth enhancement of 15% in C4 grasses compared with 23% in C3 grasses on doubling [CO2] over the present level.

The photosynthetic pathway partially explains growth responses to CO2, but CO2 effects on transpiration and plant water-use efficiency (WUE; biomass produced per unit of transpiration) will be at least as important as photosynthetic metabolism in the future productivity of rangelands. Stomata of most plant species partially close as [CO2] increases (Field et al., 1995; Drake et al., 1997). As this partial closure tends to reduce transpiration more than photosynthesis, leaf-level WUE (photosynthesis/transpiration) rises with [CO2] (Polley et al., 1996a). Reduced water loss and enhanced WUE can also be realized at the canopy level (Kirkham et al., 1991; Nie et al., 1992; Ham et al., 1995), improving plant and soil water relations (Knapp et al., 1994; Morgan et al., 1994; Wilsey et al., 1997), increasing plant production under water limitation (Owensby et al., 1993a) and lengthening the growing season (Chiariello and Field, 1996). Water relation benefits of CO2 enrichment largely explained the greater growth enhancement of C4 than C3 grasses in tallgrass prairie during dry years and the similar growth responses of C3 and C4 grasses under typically water-limiting conditions in shortgrass steppe (Owensby et al.,

1993a, 1997; Hunt et al., 1996; Coughenour and Chen, 1997). Water relation benefits also apply to annual C₃ grasslands, where effects of elevated [CO₂] on plant production are more evident in drier years (Jackson et al., 1995).

The ability to recover from defoliation is a major determinant of plant productivity and persistence on grazing lands. Recovery of grasses following grazing is controlled initially by re-mobilization of reserves, followed by photosynthetic gains (Caldwell et al., 1981). To the extent that CO₂ enrichment increases photosynthesis and storage of reserves, it should enhance recovery from grazing. Plant response to defoliation depends on complicated interactions between grazing history and the environment (Milchunas et al., 1988) and so effects of CO₂ enrichment are not likely to be simple. In a controlled environment, CO₂ enrichment had little effect on regrowth of grasses from three distinctly different grasslands (Wilsey et al., 1997).

13.3.2 Temperature

Carbon dioxide enrichment and global warming are predicted to increase net primary production on most rangelands (Baker et al., 1993; Parton et al., 1995; Coughenour and Chen, 1997; Neilson et al., 1998). Because of severe cold-temperature restrictions on growth rate and duration, warmer temperatures alone should enhance production in high- and mid-latitude and high-altitude rangelands (Baker et al., 1993; Körner et al., 1996; Rounsevell et al., 1996). Warmer temperatures should also enhance the growth response of most C3-dominated grasslands to rising [CO2] (Long, 1991; Jones and Jongen, 1996; Coughenour and Chen, 1997; Drake et al., 1997). This positive effect of warmer temperatures on production may be lessened, however, by an accompanying increase in evapotranspiration (ET) rate in drier systems such as the arid and semi-arid rangelands of Central and South America, Africa, the Middle East, Asia and Australia.

13.3.3 Precipitation

Current models yield widely varying estimates of future patterns in precipitation (Giorgi et al., 1998), making it difficult to predict consequences of altered hydrological cycles for rangelands. Productivity on most rangelands is limited by water (Campbell et al., 1997); therefore changes in the amount of precipitation will significantly impact these systems. Arid and semi-arid lands will be most sensitive to changes in precipitation, while usually wet mountain meadows will be minimally affected. Shifts in seasonal patterns of precipitation and predicted increases in storm intensity will probably have a greater impact on rangelands than shifts in precipitation amounts (Giorgi et al., 1998). It is widely agreed that storm intensity will increase, resulting in greater runoff and concentration of water in smaller portions of the landscape. Such changes could reduce productivity or increase its heterogeneity (Campbell et al., 1997; but see Williams et al., 1998). The proportion of annual precipitation that falls

during winter months is predicted to increase at high to mid-latitudes (Giorgi et al., 1998). Such a change in seasonality of precipitation, combined with warming (predicted to be greatest at high northern latitudes) and increased runoff resulting from more severe storms, could increase the incidence and severity of summer droughts in semi-arid grasslands of North America and Asia. Conversely, any increase in rainfall during the growing season will help to mitigate the desiccating effects of warmer temperatures.

13.3.4 Soil feedbacks

Long-term responses of rangelands to global change ultimately depend on the soil and its ability to supply nutrients, as well as water. Carbon dioxide enrichment appears to improve the efficiency with which plants utilize nutrients for growth (Stock and Midgley, 1995; Drake $\it et al.$, 1997). Interactions between [CO2] and nutrients are complicated, however, and plant responses to CO2 enrichment may be constrained by low fertility, especially in relatively mesic environments (Sage, 1994; Stock and Midgley, 1995).

13.4 Impacts on Forage Quality

13.4.1 Plant-animal interface

Animal production on rangelands, as in other grazing systems, depends on the quality as well as the quantity of forage. Key quality parameters for rangeland forage include fibre content and concentrations of crude protein, non-structural carbohydrates, minerals and secondary toxic compounds. Ruminants require forage with about 7% crude protein (as a percentage of dietary dry matter) for maintenance, 10–14% protein for growth and 15% protein for lactation (Ulyatt et al., 1980). Optimal rumen fermentation also requires a balance between ruminally available protein and energy (Dove, 1996). The rate at which digesta pass through the rumen depends on the fibre content of forage. Increasing fibre content slows passage and reduces animal intake.

13.4.2 Atmospheric [CO₂]

Based on expected vegetation changes and known environmental effects on forage protein, carbohydrate and fibre contents (e.g. Wilson, 1982; Owensby et al., 1993b, 1996), both positive and negative changes in forage quality are possible as a result of atmospheric and climatic change (Table 13.1). Effects of CO₂ enrichment on crude protein content of forage, for example, are likely to be negative, for plant nitrogen concentration usually declines at elevated [CO₂] (Owensby et al., 1993b; Cotrufo et al., 1998). Limited evidence suggests that the decline is greater when soil nitrogen availability is low (Bowler and Press, 1996; Wilsey, 1996), implying that rising CO₂ could reduce the digestibility of

Table 13.1. Potential changes in forage quality arising from atmospheric and climatic change.

Change	Examples of positive effects on forage quality	Examples of negative effects on forage quality
Life-form distributions	Decrease in proportion of woody shrubs and increase in grasses in areas with increased fire frequency (Ryan, 1991)	Increase in proportion of woody species because of elevated CO ₂ , increases in rainfall event sizes and longer intervals between rainfall events (Stafford Smith <i>et al.</i> , 1995)
Species or functional group distributions	Increase in C_3 grasses relative to C_4 grasses with higher CO_2 (Johnson <i>et al.</i> , 1993)	Increase in proportion of C ₄ grasses relative to C ₃ grasses due to higher temperatures (Campbell <i>et al.</i> , 1996) or changes in availability of water at elevated CO ₂ (Owensby <i>et al.</i> , 1997). Increase in plants poisonous to animals
Plant biochemical properties	Increase in non-structural carbohydrates at elevated CO ₂ (Read <i>et al.</i> , 1997). Increase in crude protein with reduced rainfall	Decrease in tissue nitrogen contents and increased fibre contents as result of reduced photosynthetic protein contents at elevated CO ₂ or higher temperatures (Sage et al., 1989; Owensby et al., 1993b, 1996; Soussana et al., 1996; Read et al., 1997). No change or decrease in crude protein in regions with more summer rainfall

forages that are already of poor quality for ruminants. Such reductions in forage quality would have pronounced negative effects on animal growth, reproduction and mortality (Owensby *et al.*, 1996) and could render livestock production unsustainable unless animal diets are supplemented with N (e.g. urea, soybean meal). Concentrations of some of the plant products that are toxic to animals may also increase in a CO₂-rich environment.

13.4.3 Botanical composition and animal selectivity

Both positive and negative effects on forage quality are possible for individual species, but the total quantity of nutrients on offer to a grazing animal is determined by the relative abundances of plant species in vegetation. Carbon dioxide enrichment initially reduced crude protein content of both species in a grass-clover mixture, but the protein content of the entire sward eventually increased at elevated [CO₂] because of a greater overall proportion of high-N clover (Schenk et al., 1997). Similar effects are likely on rangelands, which contain complex mixtures of species of differing ecology and forage quality.

Ultimately, the quality of livestock diets is determined both by the quality of the forage on offer and by selectivity of animals during grazing. Research efforts have focused primarily on changes in forage quality to the near exclusion of potential changes in grazing behaviour by animals. Selective grazing is a significant feature of livestock on rangelands, where utilization is much lower than in intensively managed pastures. There is a need, therefore, to determine whether higher temperatures or other global changes will alter grazing behaviour and whether changes in grazing behaviour could compensate for a general decline in forage quality.

13.5 Impacts on Plant Species Composition

13.5.1 Importance of botanical composition

Research has emphasized global change effects on plant and ecosystem production and water balance, but changes in plant species composition could have at least as great an impact on the goods and services that rangelands provide as might changes in production. Rangelands are used primarily for grazing. For most domestic herbivores, the preferred forage is grass. Other plants, including trees, shrubs, and other broadleaf species, can lessen livestock production and profitability by reducing availability of water and other resources to grasses, making desirable plants unavailable to livestock, or physically complicating livestock management, or poisoning grazing animals (Dahl and Sosebee, 1991). The functioning of ecosystems can also be changed by addition or loss of plants which greatly affect disturbance regimes or soil resource (Vitousek, 1990). The spread of the annual grass Bromus tectorum (cheatgrass) through the intermountain region of western North America, for example, altered the frequency and timing of wildfires, and reduced establishment of perennial herbaceous species by pre-empting soil water early in the growing season (Young, 1991).

13.5.2 Environmental controls on species composition

The plant species composition of a region is largely determined by climate and soils, with fire regime, grazing and other land uses more locally important. The primary climatic control on the distribution and abundance of plants is water balance (Stephenson, 1990), especially on rangelands, where species composition is highly correlated with both the amount of water that plants use and its availability in time and space (Parton *et al.*, 1994).

13.5.3 Atmospheric [CO₂]

Carbon dioxide enrichment should slow canopy-level evapotranspiration (ET) (Drake, 1992; Ham et al., 1995) and the rate or extent of soil water depletion (Kirkham et al., 1991; Owensby et al., 1993a; Jackson et al., 1994; Field et al.,

1997), unless stomatal closure is compensated by atmospheric or other feedbacks. Plants that are less tolerant of water stress than current dominants should be favoured. Three general mechanisms may contribute to compositional changes.

- By increasing WUE, CO₂ enrichment increases maximum leaf area and competition for light (Woodward, 1993). These changes should favour progressively taller and less drought-tolerant plants (Smith and Huston, 1989).
- Slower ET minimizes the decline in soil moisture during periods between rainfall events. Wetter soils should enhance reproduction and survival of drought-sensitive species (Jackson et al., 1995; Chiariello and Field, 1996).
- 3. By fostering wetter soils, CO₂ enrichment may increase deep percolation of water and favour more deeply rooting plants, like trees and shrubs, at the expense of shallow-rooting grasses (Polley et al., 1997). Percolation below 1 m in California sandstone grassland increased by 20% on doubling [CO₂], despite a concomitant 20% increase in plant biomass (Jackson et al., 1998).

Paradoxically, species composition may be more sensitive to a CO₂-mediated decrease in transpiration on relatively mesic rangelands (Table 13.2). Water savings are reduced when leaf area or soil evaporation increase – changes that are more likely on dry rangelands with open vegetative canopies than in mesic systems with closed vegetation.

Benefits of CO₂ enrichment to droughted plants may not be restricted to slower ET and soil water depletion. Higher [CO₂] can also extend seedling survival during drought (Polley et al., 1996b). The full impact of this effect remains to be established, but density of the dominant species in California annual grassland (Avena barbata) was 87% greater at elevated than ambient [CO₂] during a dry year, apparently because of greater survivorship (Jackson et al., 1995).

13.5.4 Precipitation regimes

A warmer climate means a more intense hydrological cycle, accompanied by an increase in the frequency of extreme events such as heavy rains and

Table 13.2. Predicted effects of CO₂ enrichment on soil water content and components of the hydrological cycle on arid and relatively mesic rangelands.

Parameter	Mesic rangelands	Arid rangelands
Transpiration/leaf area	Reduced	Reduced
Leaf area	Increased during dry periods	Increased
Total transpiration	Reduced, especially when wet	Small reduction
Soil evaporation	Little change	Possible increase
Percolation	Increased	No change
Runoff	Possible increase	No change
Soil water content		
Shallow	Increased	Small or no increase
Deep	Potentially increased	No change

droughts. Changes in the timing and intensity of rainfall will be especially important on arid rangelands, where plant community dynamics are 'event-driven' (Walker, 1993; Wiegand et al., 1995) and the seasonality of precipitation determines which plant growth strategies are successful (Westoby, 1980). The timing of precipitation also affects the vertical distribution of soil water, which controls the relative abundances of plants that root at different depths (Ehleringer et al., 1991; Weltzin and McPherson, 1997).

13.5.5 Temperature

Temperature influences botanical composition in several ways. Global warming, for example, may favour C₄ over C₃ grasses (Field and Forbe, 1990; Epstein *et al.*, 1997) by increasing the minimum daily temperature during the growing season (Teeri and Stowe, 1976) or by increasing photorespiration and reducing quantum yield in C₃ species (Ehleringer *et al.*, 1997). However, the effect of CO₂ enrichment on quantum yield is opposite to that of higher temperature. Doubling [CO₂] can, in fact, more than offset the decline in quantum yield of C₃ plants caused by a 2°C rise in temperature (Long, 1991) and render C₃/C₄ distributions and abundances relatively insensitive to the effects of higher temperature on quantum yield.

Extreme temperatures could become more frequent with global warming and could influence species distributions and abundances by affecting plant reproduction, competitive ability or survivorship. Plant responses to extreme temperatures appear to be species-specific, and thus are difficult to predict (Coleman et al., 1991; Bassow et al., 1994).

13.5.6 Interactions between temperature and [CO₂]

Many of the influences of higher temperature and [CO₂] on plants are not additive, so combined effects are not readily predictable from knowledge of individual effects (Bazzaz et al., 1996). Neither do plants respond as predictably to temperature or CO₂ as to other factors or resources (e.g. water, nitrogen). Species within a given growth form responded similarly to changes in nutrient availability and light in tussock tundra, but showed no consistent response to higher temperature (Chapin et al., 1995). Progress in predicting the response of vegetation to a warmer climate may require a better understanding of indirect effects of temperature on soil resources to which species respond more predictably (Chapin et al., 1995). Warming in montane vegetation produced species changes apparently explained by temperature effects on soil moisture (Harte and Shaw, 1995).

13.5.7 Changes on global and regional scales

Long-term and global-scale responses of vegetation to higher [CO₂] and temperature have been estimated by modelling the equilibrium distribution of earth's vegetation from hydrological and plant physiological parameters (Woodward, 1993; Neilson, 1995; Haxeltine and Prentice, 1996). Both the MAPSS (Neilson, 1995) and BIOME3 (Haxeltine and Prentice, 1996) models predict a mean increase in leaf area index of earth's vegetation following a doubling in [CO₂] (Neilson *et al.*, 1998). The total area of grassland and shrubland in simulations either remains unchanged or increases by as much as 27%, depending on the scenario modelled.

Regional-scale estimates of climate change and associated impacts are highly uncertain. Climate models generally predict a greater-than-average increase in temperature in southern Europe and central North America, accompanied by reduced precipitation and soil moisture during summer (Giorgi et al., 1998). Precipitation is particularly difficult to predict at regional scales, but there is some consensus that winter precipitation will increase at mid-latitudes. In regions like the southwestern USA, increased winter precipitation could favour large and deep-rooting woody plants over shallow-rooting warm-season grasses (Weltzin and McPherson, 1997). Wetter winters during the recent past may already have contributed to invasion of desert communities in Arizona, USA, by red brome (Bromus rubens), a winter annual (Betancourt, 1996) and of grasslands in the southwestern USA by shrubs (Neilson, 1986).

13.5.8 Local and short-term changes

The ability to predict vegetation change declines at lower spatial and temporal scales, i.e. as greater details of vegetation dynamics are required. There are at least two reasons. Firstly, transient responses of vegetation to global change depend on how quickly various species can disperse propagules across landscapes that are sometimes fragmented. Secondly, disturbances, biotic interactions and other local-scale processes become more important in vegetation dynamics at lower spatial and temporal scales.

Of necessity, field experiments with different CO₂ concentrations and temperatures are conducted at local scales, where variability in vegetation is high. Nevertheless, patterns of vegetation response are beginning to emerge.

- Directional shifts in the composition of vegetation occur most consistently when global change treatments alter water availability (Owensby et al., 1993a; Harte and Shaw, 1995; Chiariello and Field, 1996).
- Carbon dioxide enrichment usually alters species abundances in multispecies communities, even when there is no net stimulation of total biomass (Körner, 1996).
- 3. Plant response to [CO₂] or temperature in multispecies communities is not readily predictable from the response of individually grown plants or from plant morphology or physiology (Chapin et al., 1995; Körner, 1995; Leadley and Körner, 1996). This occurs because expression of the multiple direct and indirect effects of [CO₂] and temperature on plant growth and development depends on complex interactions among other environmental and biotic factors.

- As a consequence of the above, species response to [CO₂] and temperature is often highly context-specific (Roy et al., 1996).
- 5. Vegetation dynamics may be as sensitive to the secondary or indirect effects of atmospheric and climatic change as to direct effects of global changes on plant growth. In closed-canopy vegetation in particular (Roy et al., 1996), changes in dominance may correlate better with changes in plant morphology, development and phenology than with more direct effects of [CO₂] or temperature on growth (Reekie and Bazzaz, 1989). At larger scales, effects of atmospheric and climatic change on fire frequency and intensity and on soil water and N availability will probably influence botanical composition to a much greater extent than global change effects on production.
- 6. Effects of CO₂ enrichment on species composition and the rate of species change will probably be greatest in disturbed or early-successional communities where nutrient and light availability are high and species change is more highly influenced by growth-related parameters (Arnone, 1996).
- 7. Rangeland vegetation will be influenced more by management practices (land use) than by atmospheric and climatic change. Global change effects will be superimposed on and modify those resulting from land use patterns in ways that are as yet uncertain.

Vegetation changes of greatest concern to managers are those that are essentially irreversible within the constraints of traditional management, and that fundamentally alter rangeland structure and function. Such shifts between 'alternate stable states' of vegetation usually occur when changes in soil properties, disturbance regimes or animal populations remove limitations on increasing plants or create or enforce limitations on current dominants.

Vegetation change can occur gradually, as when woody plants replace grasses following prolonged grazing, but can also occur rapidly, as when a threshold of soil loss is crossed that prevents continued dominance by current occupants of a site (Friedel, 1991). Gradual vegetation change is more common on mesic grazing lands, whereas rapid or 'episodic' change is more prevelant on arid rangelands (Walker, 1993; Wiegand et al., 1995). Changes in precipitation could cause rapid shifts in vegetation on arid rangelands, but global change will more often influence the susceptibility of vegetation to other factors than directly alter the 'state' of vegetation. Unfortunately, there is no universal method for recognizing the proximity of rangelands to thresholds of vegetation change or for predicting global change effects on the susceptibility of rangelands to change.

13.6 Management Implications

13.6.1 Rangelands managed for livestock production

Global change has implications for both land managers and national or regional policy-makers. Some effects of atmospheric and climatic change can be accommodated quite easily by each group. Others will require changes in practices and policies. Anticipated changes in forage quality and quantity, for example, are not likely to be novel, and could be dealt with by feeding supplements, albeit at an economic cost. Modest shifts in primary productivity could be accommodated by adjusting stocking rates, while climatic impacts on pests and diseases might require a shift in livestock type or breed. On the other hand, innovation and changes in management practices may be required to deal with substantial changes in plant composition, including invasions by different forage species or changes to non-forage species such as trees and shrubs.

These factors could create systematic changes in enterprise profitability, with consequences for regional economies. A simulation study of a beef cattle ranch in northern Australia (Campbell et al., 1997) demonstrated the relative effects of different factors on whole-enterprise profitability (Table 13.3). The precise figures should be given no significance, because they are strongly dependent on enterprise, management and markets, but they make two important points.

- Changes in pasture composition may have a far greater effect on profitfability than changes in plant productivity.
- 2. Modest shifts in prices will affect profitability as much as other changes.

Rangeland managers already must cope with highly variable physical and marketing environments. Any factor that reduces variability should simplify management and potentially increase profitability. A decrease in interannual variability of forage production, for instance, could benefit profitability, whether the decrease results from changes in plant growth patterns or from

Table 13.3. Simulated impact of global changes on profitability of a commercial cattle ranch in northern Australia (Campbell *et al.*, 1997, supplemented with more recent unpublished simulations). Simulations ran for 100 years with realistic weather and with constant management strategy, costs and prices. Results are the change from a baseline simulation for an enterprise with annual turnover of Aus\$450,000.

Parameter impacted	Implementation	Change in annual profit (Aus\$'000s)
Plant productivity Assumes the maximal realistic effect of CO ₂ on transpiration, nitrogen and radiation use efficiency (a substantial part of the benefit results from reduced interannual variability)		+37
Forage composition	20% reduction in perennial grasses	-60
Tree/grass balance	2.5% increase in tree basal area with consequent reduction in forage production	-107
Forage quality	10% decrease in liveweight gain per year (this could be compensated by supplements)	-35
Sale prices	10% increase in sale prices	+82
Transport costs	10% increase in direct fuel costs	-2

changes in climate (Campbell et al., 1997). On the other hand, profitability could be reduced by climatic changes (such as a greater incidence of drought) that increase variability in forage production. Given the variety of environments on rangelands, we should expect the relative importance of various global change effects to differ among regions. Indeed, interannual variability is of greater concern on arid than mesic rangelands, while the anticipated decline in forage quality will be a greater problem in infertile than fertile environments (Table 13.4).

At the regional scale, then, it is clear that there could be systematic changes in profitability. We are, however, only beginning to acquire the information and to develop the tools necessary to predict these changes reliably. The simulation approach described above could be expanded to consider regional implications of changes for rangeland profitability. Baker et al. (1993) described such an effort for the western USA, while Campbell et al. (1996) described a general approach for assessing the management implications and economic consequences of global change. To provide relevant information, global change studies must focus on issues appropriate to different regions. In general, however, global change effects on diet quality and vegetation composition are the two areas of poorest knowledge.

13.6.2 Rangelands managed for other uses

Rangeland issues of greatest concern to society will differ among regions and may not include livestock production. Results of an informal survey of policy-makers in northern Australia and the western USA, for example, clearly demonstrate that livestock productivity is but one of a suite of concerns in a changing world (Table 13.5). In general, commercial rangelands of the world are tending towards less intensive grazing by livestock, with increased emphasis on other uses such as urbanization (USA), game ranching (South Africa, USA) and the transfer of former homelands to indigenous peoples

Table 13.4. Atmospheric change and its management implications for rangelands that continue to be used for grazing.

System description	Fertile	Infertile
Subhumid/ subtropical	Drop in forage quality, but probably easily compensated for at a cost with supplements; risk of shifting tree/grass balance	Drop in forage quality most significant. May cause marginal areas to be taken out of production
Arid	Increase in WUE and consequent reduction in variability of plant production between years significantly improves reliability and profitability	Minor reduction in variability and increase in production efficiency

(South Africa, Australia). Global change effects on species composition are likely to be more important than those on production in these rangelands (Table 13.6). Meanwhile, rangelands utilized for subsistence (such as those in the Sahel, the Thar Desert in India, and the margins of China) are being used more intensively to meet the needs of expanding human populations. Changes in plant production are the dominant concern in these areas.

Table 13.5. Issues raised by policy-makers for commercial rangelands of Australia and USA (unpublished data, Mark Stafford Smith, Jack Morgan).

Australia	USA
Woodland thickening	Aging of agricultural population
Costs and impacts of supplementary feeding	Urbanization and increasing land use conflict
Industry viability on marginal lands – grazing vs. cropping	Consumptive vs. non-consumptive uses of wildlife
Fire frequencies and degradation risks	Recreation interests
Opportunities for carbon sequestration	Water quality and supply
Changing drought frequency and tax incentives for managing it	Plant species migration
Regional conservation of biodiversity	Government fees and incentives on public and private land uses

Table 13.6. Implications of global change for regions where land use is dominated by intensification vs. land abandonment.

General land use pressure	Implications of global change
Intensification (Africa, China, Asia, etc.)	Rising population places more intensive demands on food production
	Effects of atmospheric changes will vary across systems (see Table 13.4) and depend greatly on regional climate change. Effects on plant production will be important,
	but compositional change towards woody plants is not likely to be a problem, given human needs for fuel wood
Reduction in grazing (USA, Australia, Europe, some of S. Africa, some of S. America)	Abandonment or substantial reduction in stocking rates tends to reduce the amount of rangeland used for live- stock production and the intensity of land use. Both changes lead to greater game ranching, tourism, nature conservation, etc.
	Most direct atmospheric effects will be unimportant for primary land uses (e.g. tourism, hunting), although non-domestic grazers may suffer from diet quality reductions. Increases in trees and shrubs could decrease fire, while greater fuel production could increase fire frequency

13.6.3 Management implications - summary

On commercial rangelands, profitability may change and management may have to be adjusted to accommodate vegetation change. The general need to optimize stocking rates will continue to be essential, and flexibility in management will remain important. The rate at which management must adjust to accommodate climatic and atmospheric change will be considerably slower than adjustments required to track market fluctuations and other aspects of the normal operating environment. The situation will differ on marginal rangelands. On the productive margins, land use pressures are likely to cause substitution by attempts at cropping. On the least productive margins, changes in profitability may tilt land use decisions in favour of or against grazing, depending on local conditions. In general, however, land use decisions on marginal rangelands will be driven by factors other than global change effects on plant and animal productivity – these will simply serve to enhance or delay existing trends.

13.7 Conclusions

Of the global change effects discussed here, none is potentially more significant for rangelands than a shift in botanical composition. Yet species change is also among the most difficult of global change effects to predict, because it is highly context-specific at the spatial and temporal scales of field experiments. What is needed is a more systematic examination of the ways in which global changes interact with and modify the characteristics of plants that determine their responses to disturbances and environmental conditions. Vegetation change will probably be more closely coupled to changes in soil resources than to immediate physiological responses of plants to [CO₂] concentration or temperature. Understanding how soil resources respond to global change is thus also a priority. Predicting and adapting to these changes are among the major challenges faced by rangeland scientists, land managers and policy-makers.

Acknowledgements

This chapter benefited greatly from the comments and input of Debra Coffin, Justin Derner, Rodney Pennington, Charles Tischler, Jake Weltzin and Brian Wilsey.

References

Alcamo, J., Kreileman, G.J.J., Bollen, J.C., van den Born, G.J., Gerlagh, R., Krol, M.S., Toet, A.M.C. and de Vries, H.J.M. (1996) Baseline scenarios of global environmental change. Global Environmental Change 6, 261–303.

- Allen-Diaz, B. (1996) Rangelands in a changing climate: impacts, adaptations, and mitigation. In: Watson, R.T., Zinyowera, M.C., Moss, R.H. and Dokken, D.J. (eds) Climate Change 1995 – Impacts, Adaptations and Mitigation of Climate Change: Scientific-Technical Analyses. Cambridge University Press, New York, pp. 130–158.
- Arnone, J.A. III (1996) Predicting responses of tropical plant communities to elevated CO₂: lessons from experiments with model ecosystems. In: Körner, Ch. and Bazzaz, F.A. (eds) Carbon Dioxide, Populations, and Communities. Academic Press, San Diego, pp. 101–121.
- Baker, B.B., Hanson, J.D., Bourdon, R.M. and Eckert, J.B. (1993) The potential effects of climate change on ecosystem processes and cattle production on US rangelands. Climatic Change 25, 97–117.
- Bassow, S.L., McConnaughay, K.D.M. and Bazzaz, F.A. (1994) The response of temperate tree seedlings grown in elevated CO₂ atmospheres to extreme temperature events. *Ecological Applications* 4, 593–603.
- Bazzaz, F.A., Bassow, S.L., Berntson, G.M. and Thomas, S.C. (1996) Elevated CO₂ and terrestrial vegetation: implications for and beyond the global carbon budget. In: Walker, B.H. and Steffen, W.L. (eds) Global Change and Terrestrial Ecosystems. Cambridge University Press, Cambridge, UK, pp. 43–76.
- Betancourt, J.L. (1996) Long- and short-term climate influences on southwestern shrublands. In: Barrow, J.R., McArthur, E.D., Sosebee, R.E. and Taucsh, R.J. (compilers) Proceedings: Shrubland Ecosystem Dynamics in a Changing Environment. USDA Forest Service, Intermountain Research Station, Ogden, Utah, pp. 5–9.
- Bowes, G. (1993) Facing the inevitable: plants and increasing atmospheric CO₂. Annual Review of Plant Physiology and Molecular Biology 44, 309–332.
- Bowler, J.M. and Press, M.C. (1996) Effects of elevated CO₂, nitrogen form and concentration on growth and photosynthesis of a fast- and slow-growing grass. New Phytologist 132, 391–401.
- Caldwell, M.M., Richards, J.H., Johnson, D.A., Nowak, R.S. and Dzurec, R.S. (1981) Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia* 50, 14–24.
- Campbell, B.D., McKeon, G.M., Gifford, R.M., Clark, H., Stafford Smith, D.M., Newton, P.C.D. and Lutze, J.L. (1996) Impacts of atmospheric composition and climate change on temperate and tropical pastoral agriculture. In: Bouma, W.J., Pearman, G.I. and Manning, M.R. (eds) Greenbouse: Coping with Climate Change. CSIRO Publishing, Melbourne, pp. 171–189.
- Campbell, B.D., Stafford Smith, D.M. and McKeon, G.M. (1997) Elevated CO₂ and water supply interactions in grasslands: a pastures and rangelands management perspective. Global Change Biology 3, 177–187.
- Chapin, F.S. III, Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J. and Laundre, J.A. (1995) Responses of arctic tundra to experimental and observed changes in climate. *Ecology* 76, 694–711.
- Chiariello, N.R. and Field, C.B. (1996) Annual grassland responses to elevated CO₂ in multiyear community microcosms. In: Körner, C. and Bazzaz, F.A. (eds) Carbon Dioxide, Populations, and Communities. Academic Press, San Diego, pp. 139–157.
- Coleman, J.S., Rochefort, L., Bazzaz, F.A. and Woodward, F.I. (1991) Atmospheric CO₂, plant nitrogen status and the susceptibility of plants to an acute increase in temperature. *Plant, Cell and Environment* 14, 667–674.
- Cotrufo, M.F., Ineson, P. and Scott, A. (1998) Elevated CO₂ reduces the nitrogen concentration of plant tissues. Global Change Biology 4, 43–54.

- Coughenour, M.B. and Chen, D.-X. (1997) Assessment of grassland ecosystem responses to atmospheric change using linked plant–soil process models. *Ecological Applications* 7, 802–827.
- Dahl, B.E. and Sosebee, R.E. (1991) Impacts of weeds on herbage production. In: James, L.F., Evans, J.O., Ralphs, M.H. and Child, R.D. (eds) Noxious Range Weeds. Westview Press, Boulder, Colorado, pp. 153–164.
- Dove, H. (1996) The ruminant, the rumen and the pasture resource: nutrient interactions in the grazing animal. In: Hodgson, J. and Illius, A.W. (eds) The Ecology and Management of Grazing Systems. CAB International, Wallingford, UK, pp. 219–246.
- Drake, B.G. (1992) A field study of the effects of elevated CO₂ on ecosystem processes in a Chesapeake Bay wetland. Australia Journal of Botany 40, 579–595.
- Drake, B.G., Gonzàlez-Meler, M.A. and Long, S.P. (1997) More efficient plants: a consequence of rising atmospheric CO₂? Annual Review of Plant Physiology and Molecular Biology 48, 609–639.
- Ehleringer, J.R., Phillips, S.L., Schuster, W.S.F. and Sandquist, D.R. (1991) Differential utilization of summer rains by desert plants. *Oecologia* 88, 430–434.
- Ehleringer, J.R., Cerling, T.E. and Helliker, B.R. (1997) C₄ photosynthesis, atmospheric CO₂, and climate. Oecologia 112, 285–299.
- Epstein, H.E., Lauenroth, W.K., Burke, I.C. and Coffin, D.P. (1997) Productivity patterns of C₃ and C₄ functional types in the US Great Plains. *Ecology* 78, 722–731.
- Field, C.B., Jackson, R.B. and Mooney, H.A. (1995) Stomatal responses to increased CO₂: implications from the plant to the global scale. *Plant, Cell and Environment* 18, 1214–1225.
- Field, C.B., Lund, C.P., Chiariello, N.R. and Mortimer, B.E. (1997) CO₂ effects on the water budget of grassland microcosm communities. Global Change Biology 3, 197–206.
- Field, T.R.O. and Forbe, M.B. (1990) Effects of climate warming on the distribution of C₄ grasses in New Zealand. Proceedings of the New Zealand Grassland Association 51, 47–50.
- Friedel, M.H. (1991) Range condition assessment and the concept of thresholds: a viewpoint. Journal of Range Management 44, 422–426.
- Ghannoum, O., von Caemmerer, S., Barlow, E.W.R. and Conroy, J.P. (1997) The effect of CO₂ enrichment and irradiance on the growth, morphology and gas exchange of a C₃ (Panicum laxum) and a C₄ (Panicum antidotale) grass. Australian Journal of Plant Physiology 24, 227–237.
- Giorgi, R., Meehl, G.A., Kattenberg, A., Grassl, H., Mitchell, J.F.B., Stouffer, R.J., Tokioka, T., Weaver, A.J. and Wigley, T.M.L. (1998) Simulation of regional climate change with global coupled climate models and regional modelling techniques. In: Watson, R.T., Zinyowera, M.C., Moss, R.H. and Dokken, D.J. (eds) The Regional Impacts of Climate Change: an Assessment of Vulnerability. Cambridge University Press, New York, pp. 427–437.
- Ham, J.M., Owensby, C.E., Coyne, P.I. and Bremer, D.J. (1995) Fluxes of CO₂ and water vapor from a prairie ecosystem exposed to ambient and elevated atmospheric CO₂. Agricultural and Forest Meteorology 77, 73–93.
- Harte, J. and Shaw, R. (1995) Shifting dominance within a montane vegetation community: results of a climate-warming experiment. Science 267, 876–880.
- Haxeltine, A. and Prentice, I.C. (1996) BIOME3: an equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability and competition among plant functional types. Global Biogeochemical Cycles 10, 693–710.

- Hunt, H.W., Elliott, E.T., Detling, J.K., Morgan, J.A. and Chen, D.-X. (1996) Responses of a C₃ and a C₄ perennial grass to elevated CO₂ and temperature under different water regimes. Global Change Biology 2, 35–47.
- Jackson, R.B., Sala, O.E., Field, C.B. and Mooney, H.A. (1994) CO₂ alters water use, carbon gain, and yield for the dominant species in a natural grassland. *Oecologia* 98, 257–262.
- Jackson, R.B., Luo, Y., Cardon, Z.G., Sala, O.E., Field, C.B. and Mooney, H.A. (1995) Photosynthesis, growth and density for the dominant species in a CO₂-enriched grassland. *Journal of Biogeography* 22, 221–225.
- Jackson, R.B., Sala, O.E., Paruelo, J.M. and Mooney, H.A. (1998) Ecosystem water fluxes for two grasslands in elevated CO₂: a modelling analysis. *Oecologia* 113, 537–546.
- Johnson, H.B., Polley, H.W. and Mayeux, H.S. (1993) Increasing CO₂ and plant-plant interactions: effects on natural vegetation. Vegetatio 104/105, 157-170.
- Jones, M.B. and Jongen, M. (1996) Sensitivity of temperate grassland species to elevated atmospheric CO₂ and the interaction with temperature and water stress. Agricultural and Food Science in Finland 5, 271–283.
- Karl, T.R. (1998) Regional trends and variations of temperature and precipitation. In: Watson, R.T., Zinyowere, M.C. and Moss, R.H. (eds) The Regional Impacts of Climate Change: an Assessment of Vulnerability. Cambridge University Press, New York, pp. 413–425.
- Kirkham, M.B., He, H., Bolger, T.P., Lawlor, D.J. and Kanemasu, E.T. (1991) Leaf photosynthesis and water use of big bluestem under elevated carbon dioxide. Crop Science 31, 1589–1594.
- Knapp, A.K., Fahnestock, J.T. and Owensby, C.E. (1994) Elevated atmospheric CO₂ alters stomatal responses to variable sunlight in a C₄ grass. *Plant, Cell and Environment* 17, 189–195.
- Körner, Ch. (1995) Biodiversity and CO2: global change is under way. Gaia 4, 234-243.
- Körner, Ch. (1996) The response of complex multispecies systems to elevated CO₂. In: Walker, B.H. and Steffen, W.L. (eds) Global Change and Terrestrial Ecosystems. Cambridge University Press, Cambridge, UK, pp. 20–42.
- Körner, Ch., Diemer, M., Schäppi, B. and Zimmermann, L. (1996) Response of alpine vegetation to elevated CO₂. In: Koch, G.W. and Mooney, H.A. (eds) Carbon Dioxide and Terrestrial Ecosystems. Academic Press, San Diego, pp. 177–196.
- Leadley, P.W. and Körner, Ch. (1996) Effects of elevated CO₂ on plant species dominance in a highly diverse calcareous grassland. In: Körner, Ch. and Bazzaz, F.A. (eds) Carbon Dioxide, Populations, and Communities. Academic Press, San Diego, pp. 159–175.
- LeCain, D.R. and Morgan, J.A. (1998) Growth, photosynthesis, leaf nitrogen and carbohydrate concentrations in NAD-ME and NADP-ME C₄ grasses grown in elevated CO₂. Physiologia Plantarum 102, 297–306.
- Long, S.P. (1991) Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO₂ concentrations: has its importance been underestimated? Plant, Cell and Environment 14, 729–739.
- Milchunas, D.G., Sala, O.E. and Lauenroth, W.K. (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* 132, 87–106.
- Morgan, J.A., Knight, W.G., Dudley, L.M. and Hunt, H.W. (1994) Enhanced root system C-sink activity, water relations and aspects of nutrient acquisition in mycotrophic Bouteloua gracilis subjected to CO₂ enrichment. Plant and Soil 165, 139–146.

Neilson, R.P. (1986) High-resolution climatic analysis and southwest biogeography. Science 232, 27–34.

- Neilson, R.P. (1995) A model for predicting continental-scale vegetation distribution and water balance. *Ecological Applications* 5, 362–385.
- Neilson, R.P., Prentice, I.C., Smith, B., Kittel, T. and Viner, D. (1998) Simulated changes in vegetation distribution under global warming. In: Watson, R.T., Zinyowere, M.C. and Moss, R.H. (eds) The Regional Impacts of Climate Change: an Assessment of Vulnerability. Cambridge University Press, New York, pp. 439–456.
- Nie, D., He, H., Mo, G., Kirkham, M.B. and Kanemasu, E.T. (1992) Canopy photosynthesis and evapotranspiration of rangeland plants under doubled carbon dioxide in closed-top chambers. Agricultural and Forest Meteorology 61, 205–217.
- Owensby, C.E., Coyne, P.I., Ham, J.M., Auen, L.A. and Knapp, A.K. (1993a) Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated CO₂. Ecological Applications 3, 644–653.
- Owensby, C.E., Coyne, P.I. and Auen, L.M. (1993b) Nitrogen and phosphorus dynamics of a tallgrass prairie ecosystem exposed to elevated carbon dioxide. *Plant, Cell and Environment* 16, 843–850.
- Owensby, C.E., Cochran, R.C. and Auen, L.M. (1996) Effects of elevated carbon dioxide on forage quality for ruminants. In: Körner, Ch. and Bazzaz, F.A. (eds) Carbon Dioxide, Populations and Communities. Academic Press, San Diego, pp. 363–371.
- Owensby, C.E., Ham, J.M., Knapp, A.K., Bremner, D. and Auen, L.M. (1997) Water vapour fluxes and their impact under elevated CO₂ in a C₄-tallgrass prairie. Global Change Biology 3, 189–195.
- Parton, W.J., Ojima, D.S. and Schimel D.S. (1994) Environmental change in grasslands: assessment using models. Climatic Change 28, 111–141.
- Parton, W.J., Scurlock, J.M.O., Ojima, D.S., Schimel, D.S., Hall, D.O. and Scopegram Group Members (1995) Impact of climate change on grassland production and soil carbon worldwide. Global Change Biology 1, 13–22.
- Polley, H.W., Johnson, H.B., Mayeux, H.S., Brown, D.A. and White, J.W.C. (1996a) Leaf and plant water use efficiency of C₄ species grown at glacial to elevated CO₂ concentrations. *International Journal of Plant Sciences* 157, 164–170.
- Polley, H.W., Johnson, H.B., Mayeux, H.S., Tischler, C.R. and Brown, D.A. (1996b) Carbon dioxide enrichment improves growth, water relations and survival of droughted honey mesquite (*Prosopis glandulosa*) seedlings. *Tree Physiology* 16, 817–823.
- Polley, H.W., Mayeux, H.S., Johnson, H.B. and Tischler, C.R. (1997) Viewpoint: atmospheric CO₂, soil water, and shrub/grass ratios on rangelands. *Journal of Range Management* 50, 278–284.
- Read, J.J., Morgan, J.A., Chatterton, N.J. and Harrison, P.A. (1997) Gas exchange and carbohydrate and nitrogen concentrations in leaves of *Pascopyrum smithii* (C₃) and *Bouteloua gracilis* (C₄) at different carbon dioxide concentrations and temperatures. *Annals of Botany* 79, 197–206.
- Reekie, E.G. and Bazzaz, F.A. (1989) Competition and patterns of resource use among seedlings of five tropical trees grown at ambient and elevated CO₂. Oecologia 79, 212–222.
- Rounsevell, M.D.A., Brignall, A.P. and Siddons, P.A. (1996) Potential climate change effects on the distribution of agricultural grassland in England and Wales. Soil Use and Management 12, 44–51.
- Roy, J., Guillerm, J.-L., Navas, M.-L. and Dhillion, S. (1996) Responses to elevated CO₂ in Mediterranean old-field microcosms: species, community, and ecosystem components. In: Körner, Ch. and Bazzaz, F.A. (eds) Carbon Dioxide, Populations, and Communities. Academic Press, San Diego, pp. 123–138.

- Ryan, K.C. (1991) Vegetation and wildland fire: implications of global climate change. Environment International 17, 169–178.
- Sage, R.F. (1994) Acclimation of photosynthesis to increasing atmospheric CO₂: the gas exchange perspective. Photosynthesis Research 39, 351–368.
- Sage, R.F., Sharkey, T.D. and Seeman, J.R. (1989) Acclimation of photosynthesis to CO₂ in five C₃ species. Plant Physiology 89, 590–596.
- Schenk, U., Jager, H.-J. and Weigel, H.-J. (1997) The response of perennial ryegrass/white clover mini-swards to elevated atmospheric CO₂ concentrations: effects on yield and fodder quality. Grass and Forage Science 52, 232–241.
- Smith, T. and Huston, M. (1989) A theory of the spatial and temporal dynamics of plant communities. Vegetatio 83, 49–69.
- Soussana, J.F., Casella, E. and Loiseau, P. (1996) Long-term effects of CO₂ enrichment and temperature increase on a temperate grass sward. II. Plant nitrogen budgets and root fraction. *Plant and Soil* 182, 101–114.
- Stafford Smith, M. (1996) Management of rangelands: paradigms at their limits. In: Hodgson, I. and Illius, A.W. (eds) The Ecology and Management of Grazing Systems. CAB International, Wallingford, UK, pp. 325–357.
- Stafford Smith, M., Campbell, B.D., Archer, S. and Steffen, W. (1995) GCTE Focus 3 Pastures and Rangelands Network: an Implementation Plan. Global Change and Terrestrial Ecosystems Report No. 3, CSIRO, Canberra, Australia, 59 pp.
- Stephenson, N.L. (1990) Climatic control of vegetation distribution: the role of the water balance. American Naturalist 135, 649–670.
- Stock, W.D. and Midgley, G.F. (1995) Ecosystem response to elevated CO₂: nutrient availability and nutrient cycling. In: Moreno, J.M. and Oechel, W.C. (eds) Global Change and Mediterranean-type Ecosystems. Ecological Studies 117. Springer-Verlag, New York, pp. 326–342.
- Stoddart, L.A., Smith, A.D. and Box, T.W. (1975) Range Management. McGraw-Hill, New York, 532 pp.
- Teeri, J.A. and Stowe, L.G. (1976) Climatic patterns and the distribution of C₄ grasses in North America. Oecologia 23, 1–12.
- Ulyatt, M.J., Fennessy, P.F., Rattray, P.V. and Jagush, K.T. (1980) The nutritive value of supplements. In: Drew, K.R. and Fennesy, P.F. (eds) Supplementary Feeding. New Zealand Society of Animal Production, Mosgeil, New Zealand, pp.157–184.
- Vitousek, P.M. (1990) Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57, 7–13.
- Walker, B.H. (1993) Rangeland ecology: understanding and managing change. Ambio 22, 80–87.
- Weltzin, J.F. and McPherson, G.R. (1997) Spatial and temporal soil moisture resource partitioning by trees and grasses in a temperate savanna, Arizona, USA. Oecologia 112, 156–164.
- Westoby, M. (1980) Elements of a theory of vegetation dynamics in arid rangelands. Israel Journal of Botany 28, 169–194.
- Wiegand, T., Milton, S.J. and Wissel, C. (1995) A simulation model for a shrub ecosystem in the semiarid Karoo, South Africa. Ecology 76, 2205–2221.
- Williams, K.J., Wilsey, B.J., McNaughton, S.J. and Banyikwa, F.F. (1998) Temporally variable rainfall does not limit yields of Serengeti grasses. Oikos 81, 463–470.
- Wilsey, B.J. (1996) Urea additions and defoliation affect plant responses to elevated CO₂ in a C₃ grass from Yellowstone National Park. Oecologia 108, 321–327.
- Wilsey, B.J., Coleman, J.S. and McNaughton, S.J. (1997) Effects of elevated CO₂ and defoliation on grasses: a comparative ecosystem approach. *Ecological Applications* 7, 844–853.

- Wilson, J.R. (1982) Environmental and nutritional factors affecting herbage quality. In: Hacker, J.B. (ed.) Nutritional Limits to Animal Production from Pastures. Commonwealth Agricultural Bureaux, Farnham Royal, UK, pp. 111–131.
- Woodward, F.I. (1993) Leaf response to the environment and extrapolation to larger scales. In: Solomon, A.M. and Shugart, H.H. (eds) Vegetation Dynamics and Global Change. Chapman & Hall, New York, pp. 71–100.
- Young, J.A. (1991) Cheatgrass. In: James, L.F., Evans, J.O., Ralphs, M.H. and Child, R.D. (eds) Noxious Range Weeds. Westview, Boulder, Colorado, pp. 408–418.